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SEXUAL DIFFERENCES IN CONSPECIFIC TERRITORIAL DEFENSE OF MARSH HARRIERS (*Circus aeruginosus*)

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ABSTRACT.—Observations of six pairs of marsh harriers (*Circus aeruginosus*) in the Upper Ebro Valley (Navarra, Spain) during the incubation and nestling periods showed that: (1) males defended their territories against conspecific intruders more often than females, (2) responses were more frequent to intrasexual as opposed to intersexual intrusions, and (3) frequency of responses between opposite sexes increased when the breeding season progressed. The greater rate of defensive responses of males toward other males and tolerance of females by males at the onset of reproduction supported the idea that conspecific territorial defense during the breeding season functions to protect the nesting area and the pair bond. Alternatively, sex difference may reflect differences in the costs of defense in relation with aerial agility of the sex.

KEY WORDS: Circus aeruginosus; *Marsh harrier*; *sexual differences*; *Spain*; *territoriality*.

Diferencias sexuales en el comportamiento de defensa territorial del Aguilucho lagunero (*Circus aeruginosus*)

RESUMEN.—Las observaciones realizadas en seis parejas de Aguilucho lagunero (*Circus aeruginosus*) en la cabecera del Valle del Ebro (Navarra, España) durante la incubación y la crianza de los pollos indican que: (1) los machos defienden el área de nidificación más intensamente que las hembras, (2) las respuestas defensivas intrasexuales son más frecuentes que las intersexuales, y (3) la frecuencia de las defensas contra los intrusos de sexo opuesto se incrementan conforme avanza la reproducción. Así, la defensa conespecífica puede ser interpretada como una forma de protección del área de cría y de mantenimiento de la pareja, y la tolerancia hacia el sexo opuesto al comienzo de la reproducción como una forma de asegurar una posible sustitución de la pareja. Las diferencias en la actividad defensiva observadas entre machos y hembras pueden deberse al diferente coste energético de la defensa derivado de la distinta agilidad en el vuelo de ambos sexos.

[Traducción Autores]

Variation in territorial defense among birds of prey has been the subject of many studies from which several theories have been proposed (see reviews by Regelmann and Curio 1986, Andersson and Wiklund 1987, Montgomerie and Weatherhead 1988, Redondo 1990, Wiklund 1990). Nevertheless, aspects such as the sexual differences in defense behavior among raptors with reversed sexual dimorphism has still not been studied in detail (Wiklund and Stigh 1983, Andersson and Wiklund 1987, Wiklund 1990). Moreover, studies usually focused on defense of broods against heterospecific predators (Montgomerie and Weatherhead 1988), whereas the function and performance of conspecific territorial defense has not yet been well-studied.

Recently Temeles (1986, 1989) analyzed the influence of the status and sex of conspecific intruders on the territorial response of male and female northern harriers (*Circus cyaneus*), and proposed two conspecific territorial defense models based on territory mate usurpation and food stealing. Temeles's studies were conducted during the winter and they showed that during the nonbreeding season defense by harriers ensured an adequate food supply. In contrast, territorial defense by harriers in the breeding season may function in another way, maybe to ensure a mate and/or a territory, in addition to food.

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Table 1. Sexual differences in the defense response of territorial adult marsh harriers in relation to the sex of conspecific intruders.

	OWNERS								
	MALES			FEMALES			TOTAL		
INTRUDERS	CHASED	NOT CHASED	χ^2	CHASED	NOT CHASED	χ^2	CHASED	NOT CHASED	χ^2
Males	79	17	0.19	19	35	14.96[b]	98	52	5.17[a]
Females	67	17		34	12		101	29	
Total	146	34		53	47		199	81	

Fisher's test: [a] $P < 0.05$, [b] $P < 0.001$.

The aim of our study was to examine sex differences in the territorial defense response of the marsh harrier (*Circus aeruginosus*) during the breeding period. We analyzed the intensity of responses made by male and female territory owners to male and female intruders in an area where the high concentration of breeding pairs caused frequent conspecific intrusions. Finally, we discuss possible functions of conspecific territorial defense (Temeles 1986, 1989) and how reversed size dimorphism (Andersson and Wiklund 1987) and renesting possibilities (Barash 1975, Weatherhead 1979) may affect the intensity of conspecific territorial defense by each sex.

STUDY AREA AND METHODS

The study was carried out at the Dos Reinos Reserve (Upper Ebro Valley, Spain). Due to the scarcity of wetlands and the increasing marsh harrier population in the region (Fernández 1990), the reserve supports a great concentration of nesting pairs. Eleven monogamous pairs nested in 4.2 ha of reedbed with an average nearest neighbor distance between nests 72.3 m ($N = 11$), a situation which resulted in frequent territorial interactions between neighboring pairs.

Six nesting pairs were observed simultaneously by two people from a fixed location about 500 m from the nests. Each observer, equipped with binoculars (8 × 35) and telescopes (20–45 × 60), watched three pairs and recorded the harriers' behavior on tape. The proximity of nest sites in the reedbed allowed us to observe several pairs simultaneously. Variation in plumage (color, distribution of spots and flight feathers in molt) were sketched on plates during the laying period and were used for later individual recognition of pairs. We spent 549.5 hr in 76 d observing the pairs during spring (April–June) of 1991 including the incubation (223.5 hr) and nestling periods (189.5 hr and 136.5 hr). We divided the breeding period (from egg laying to fledging) into three parts: incubation, first nestling phase (1–22 d) and second nestling phase (23–44 d), to study the variation of defense intensity between sexes. During these periods we noted all conspecific intrusions, recording the sex of the intruder and defender.

We considered as intruders only those marsh harriers that flew within 50 m of an occupied nest and lower than approximately 30 m above the ground. For each intrusion we noted the presence or absence of each member of the nesting pair in their territory. We only took into account the intrusions of adult marsh harriers when the owners were in a situation to observe and defend the territory, and excluded the intrusions of young birds and those where the owners were on the nest or with food and were unlikely to respond. We considered a response to intrusion to occur when one of the nesting pair attacked or chased the intruder. We defined an attack as a steep dive with feet dropped to within 5 m of the intruder and a chase as following a withdrawing intruder a long distance (Andersson and Wiklund 1987). Other defensive behaviors of lesser intensity or that did not include physical contact such as calls, stoops, and circling at a high altitude were not included (Wiklund and Stigh 1983, Andersson and Wiklund 1987, Picozzi 1984). To examine the differences of responses to intrusions versus no response, we used a test of Fisher's exact probability (Siegel 1956). The null hypotheses were: (1) that females respond to intrusions as strongly as males, (2) that males respond similarly to male and female conspecific intruders, and (3) that rates of defenses do not change throughout the three breeding periods considered.

RESULTS

Sexual Roles in Territorial Defense. We observed a total of 305 conspecific intrusions in which at least one harrier was present in its territory. In 280 of the cases the intruder was an adult. Attacks or chases occurred during 71.1% ($N = 199$) of the intrusions. Males responded more often than females (81.1% in males vs. 53.0% in females; Table 1). When both owners were present in the territory ($N = 48$), males responded significantly more often to conspecific intrusions (60.4%) than females (27.1%, $\chi^2 = 10.84$, $P < 0.001$; Table 2).

Males defended more against intruding males than intruding females but not significantly so (Table 1).

Table 2. Rate of intrusions defended by male and/or female marsh harriers when both owners were present in the territories.

Intruders	Number of intrusions	% of intrusions that territorial holders responded to: By males	By females	By males and/or by females	By both
Males	26	65.4	19.2	84.6	0.0
Females	22	54.6	36.4	86.4	4.6
Total	48	60.4	27.1	85.4	2.1

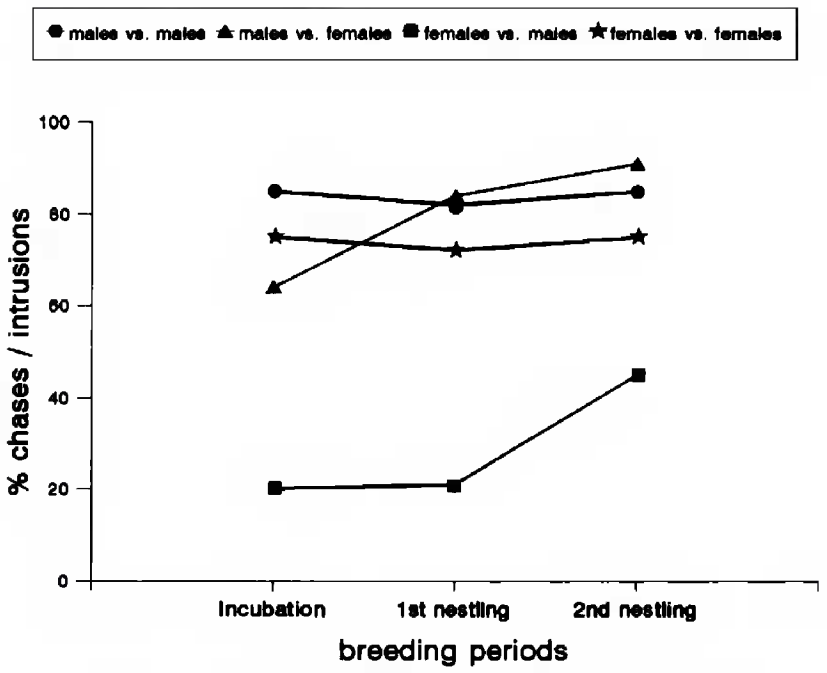

Figure 1. Sexual differences in conspecific territorial defense of marsh harriers during the breeding season.

However, females responded significantly more often to female intruders than to male intruders ($\chi^2 = 14.96$, $P < 0.001$).

Variation Throughout the Breeding Periods. The intensity of intrasexual defense remained constant throughout the incubation and nestling periods (Fig. 1). However, the proportion of defenses against the opposite sex increased during the breeding season ($\chi^2 = 9.17$, $P < 0.05$) and, although female defense against males was always low, intra- and intersexual defenses tended to become more equal as the nestling period progressed.

Discussion

Temeles (1986, 1989) proposed two not mutually exclusive hypotheses for conspecific territorial defense in the northern harrier during nonbreeding period: (1) food resource competition, and (2) territory-mate competition. In the marsh harrier we found that during breeding: (1) males defended the nest area more actively than females, (2) intrasexual defense was more common than intersexual defense, and (3) attacks and chases against the opposite sex increased during the nestling period. Competition for food could give rise to a greater intrasexual defense due to sexual dimorphism and differences in prey selection between sexes (Schipper 1978), but this provides an incomplete explanation because while intersexual defense increased during the breeding period, the intrasexual response remained constant.

Our results agree with the sex-differential interest hypothesis (Regelmann and Curio 1986) that predicts a higher investment in defense by males because of their stronger interest in territory or mate. The fact that the frequency of defenses against the opposite sex was low at the onset of the breeding season and increased thereafter could be interpreted as intersexual tolerance that favors the possibility of mate replacement. Barash (1975) and Weatherhead (1979) suggested that renesting potential could have a profound effect on the defense strategy of nesting birds. According to this hypothesis, defense should be more intense against the same sex and less for the opposite sex, since intruders of the opposite sex could potentially become mates. In this case it is logical that the territorial tolerance with regard to the opposite sex be greater in the earlier phases of the breeding season, when there is a possibility of losing clutches or broods and it still might be necessary to reinitiate breeding.

On the other hand, the greater conspecific territorial defense of males may also be related to their superior flight abilities (Wiklund and Stigh 1983, Andersson and Wiklund 1987, Wiklund 1990). Andersson and Wiklund (1987) proposed that the greater defense intensity of male raptors with reversed sexual dimorphism is based in their greater agility, explained by the inverse relation between size and agility (Andersson and Norberg 1981). Our results also support this hypothesis which predicts that male marsh harriers, being smaller (Cramp and Simmons 1980), are able to chase any size conspecific while females are only able to defend effectively against females, of their own size, and not against more agile males.

Thus, sexual differences in conspecific territorial defense in marsh harriers might be explained by: (1) territory-mate competition (Temeles 1989), which includes a greater intrasexual defense and an increase in intersexual defense during the nestling period, and (2) greater defensive capabilities among male marsh harriers, attributed to their greater agility in flight (Andersson and Wiklund 1987) which enables them to defend effectively against both male and female conspecific intruders.

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